FIRST RECORD OF *ASCOGREGARINA TAIWANENSIS* (APICOMPLEXA: LECUDINIDAE) IN NORTH AMERICAN *AEDES ALBOPICTUS*

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ABSTRACT. *Aedes albopictus* collected in the East St. Louis, Illinois, area were found infected with the gregarine protozoan, *Ascogregarina taiwanensis*. Infection rates varied from 67 to 95% at 4 sites and 0 to 10% at 2 others. Lower infection levels were found in *Ae. epactius* (42%) and *Culex restuans* (one larva). Four mosquito species were cross-infected in the laboratory with gregarines isolated from field-collected hosts. *Aedes atropalpus* was 90% susceptible to *A. taiwanensis* (100% in *Ae. albopictus*), with abnormal development and some melanization of trophozoites and gametocysts. In *Ae. aegypti* and *Cx. restuans*, the experimental infection was much lower (12–56%) and exhibited abnormalities similar to the *Ae. atropalpus* infections. *Ascogregarina* oocysts recovered from both *Ae. aegypti* and *Ae. atropalpus* hosts were subsequently infective to *Ae. albopictus*. In *Ae. triseriatus*, *A. taiwanensis* infection was very low (25%, 1–2 trophozoites per larva); gametocysts were not observed nor were infectious oocysts obtained. We conclude that *A. taiwanensis*, newly introduced to the USA with *Ae. albopictus*, can develop in 4 indigenous mosquito species and can produce deleterious effects in at least 2, *Ae aegypti* and *Ae. atropalpus*.

INTRODUCTION

The recent introduction of the Asian tiger mosquito, *Aedes albopictus* (Skuse), into the Western Hemisphere (Sprenger and Wuithiranyagool 1986, Hawley et al. 1987) is viewed with concern because of the proven capacity of this mosquito as a disease vector in Asia. It has become widespread in the central and eastern United States, with concentrations in several major cites—particularly Houston, New Orleans, Kansas City and St. Louis. In spite of substantial research interest in this mosquito involving both ecological and genetic studies (Hawley 1988), there have been no North American reports of the parasites that are normally associated with *Ae. albopictus* in its native range.

Gregarine protozoan parasites of *Ae. albopictus* were described from field collections of larvae in Taiwan as *Ascogregarina* (=*Ascocystis*) *taiwanensis* (Lien and Levine 1980). Although these protozoans have been found in other Asian *Ae. albopictus* populations, notably in India (Ray 1933), China (Feng in Vavra 1969) and Malaysia (Else and Dangsupa 1974), descriptions of their range or infection intensity have not been published. In citations previous to 1980, the *Ae. albopictus* gegarines were identified as *Ascogregarina* (=*Gregarina*, =*Lankesteria*) *culicis*, first described by Ross from *Aedes aegypti* (Linn.). However, the inability to cross-infect *Ae. aegypti* with the gregarine obtained from *Ae. albopictus* (Else and Dangsupa 1974) clearly indicated this gregarine as a distinct species (Lien and Levine 1980).

Where larval guts of field populations of other container-breeding *Aedes* species have been examined, host-specific gregarines have been found to be widespread and in high frequency. *Ascogregarina culicis* is common throughout the range of *Ae. aegypti* in the United States; *A. clarki* is found in California tree holes with its host *Ae. sierrensis* (Ludlow), and *A. barretti* has been isolated from many populations of *Ae. triseriatus* (Say) (Beier and Craig 1985).

In the following, we: 1) document the existence of *A. taiwanensis* in the United States, 2) describe its apparent pathogenicity in exotic hosts, 3) note a disjunct distribution of infected and uninfected hosts, 4) report how cross-infection experiments have supported our identification of this gregarine and associated it with its natural host and 5) indicate the potential of exotic hosts for its perpetuation.

MATERIALS AND METHODS

Collection sites: All samples (larvae, pupae and adult stages) of *Aedes albopictus* and associated gregarine were collected from Madison and St. Clair counties of Illinois in the East St. Louis area (Fig. 1). This was accomplished as part of an intensive regional survey for *Ae. albopictus* in the summer of 1988. Table 1 lists habitat parameters of sites (all with used tires) from which larvae were collected and inspected for gregarines. Well-shaded tire piles tended to have more water-containing tires and larger populations of mosquito larvae, similar to the descriptions of Beier et al. (1983); consequently, these sites were sampled more intensively. Adults were sampled both by landing-biting collections and with a battery-powered suction aspirator (Nasci 1981). Efforts were concentrated at locations where the vegetation was thick and adult mosquito density was high.

Dissection: Dissections of larvae and pupae proceeded as follows: 1) Thorax and head were separated from the abdomen on a microscope slide with a pair of minuten pins in orangewood

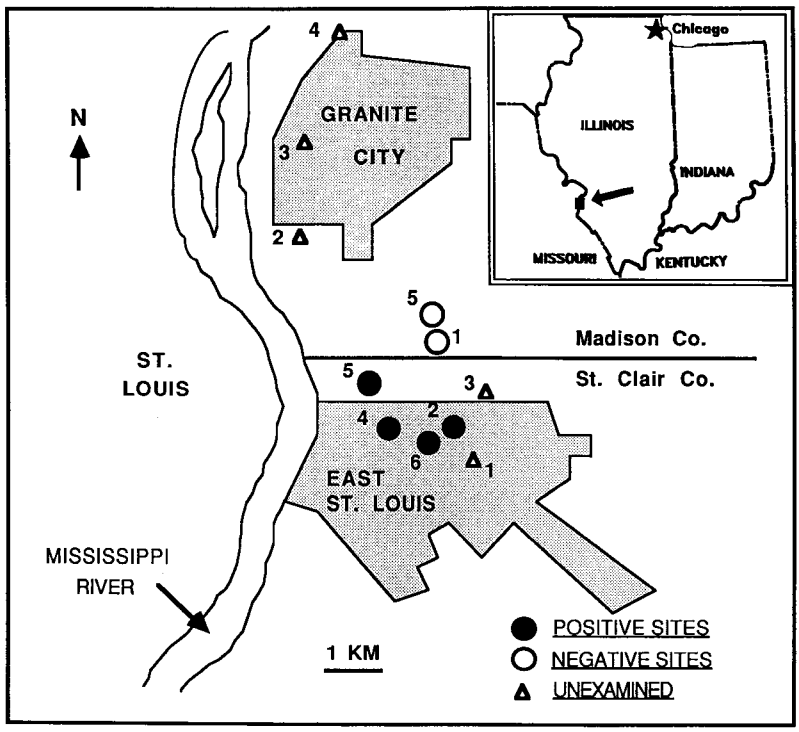

Fig. 1. Location of *Aedes albopictus* sites in the East St. Louis area, showing those positive for *Ascogregarina taiwanensis*. Sites unexamined for *Ascogregarina* had few larval habitats or had very low larval populations. (The *Ae. albopictus* sites were numbered consecutively within each county as they were discovered.)

sticks, while viewing through a dissecting microscope. 2) Contents of the abdomen were gently teased out through the anterior of the abdomen by placing pressure at the posterior abdomen and gradually pressing anteriorly. 3) The gut contents enclosed in the peritrophic membrane were pulled from inside the isolated gut. 4) Head, thorax and abdominal remains were pressed under one coverslip; gut and gut contents were covered with second coverslip. 5) Larvae were identified at 160× with a Leitz Dialux® microscope. 6) Guts and contents were scanned for gregarines at 40×, then checked at 160× with both bright-field and polarized light optics. The highly birefringent amylopectin granules of the protozoan were easily seen against a dark field. Even early (globular) stages of the gregarine were distinguishable from tissue obstructions and other granulated gut cells.

Dissection fluid under both coverslips was examined. Normally, few gregarines were found outside the isolated gut. Displacement of trophozoites and gamonts was monitored through the dissecting microscope during dissection. Movement from original positions was minimal, although increased coverslip pressure proved more disruptive.

Source of mosquito and gregarine strains: The origin and dates of collection of the laboratory strains used in the cross-infection experiments were as follows: 1) *Ae. albopictus*—3 strains, STCLAIR-2 and MADISON-1 from East St. Louis, Illinois, area (Table 1, Fig. 1), summer of 1988; NEW-ORLEANS-87 from Jefferson Parish, New Orleans, Louisiana, June 1987. 2) *Ae. aegypti*—2 strains, WACO from Waco, Texas, 1987; ROCK originally from the Rockefeller Institute, colonized for more than 50 years. 3) *Ae. atropalpus* (Coquillett)—SG strain, from St. Joseph Co., Indiana, June 1985. 4) *Ae. triseriatus*—WALTON strain, from St. Joseph Co., Indiana, June 1969. 5) *Culex restuans* Theobald—field-collected as egg rafts from tires in St. Joseph Co., Indiana, September 1988.

Two strains of *Ascogregarina taiwanensis* were used in the experimental infections. ESL was isolated from East St. Louis *Ae. albopictus* collected in the summer of 1988. The second, MALAY, originated from *Ae. albopictus* collected in Kuala Lampur, Malaysia, by W. Hawley, December 1988. A second gregarine species, *A. barretti* from *Ae. triseriatus*, was isolated from collections in St. Joseph Co., Indiana, 1987.

Oocyst isolation and mosquito infection: Following the dissection of field collected material, infected adult mosquito carcasses were pooled according to mosquito species. The method of oocyst isolation has been previously described

Table 1. Location and qualitative parameters of tire sites in the East St. Louis (Illinois) area from which larvae were dissected for *Ascogregarina*.

Site code*	Latitude/ longitude	Locality	General environment	Mosquito species identified**
Madison County				
MADISON-1	38°37′42.8″N 90°08′41.5″W	Eagle Park Rd. (Watson's Tire)	Partially shaded to open sun, thousands of tires in 2 long, 250-m parallel heaps.	ALB, EPA, TRI, PIP, SIG, RUT
MADISON-5	38°39′48.4″N 90°08′47.5″W	Eagle Park Rd. N.	50 × 12 × 2 m partially shaded pile, several hundred tires, containing much organic debris.	ALB, EPA, TER, PUN
St. Clair County				
STCLAIR-2	38°38′08.0″N 90°08′13.3″W	9th and Lynch Ave.	Shaded by large trees along freeway; 75–100 tires, weedy.	ALB, EPA, PIP, PUN
STCLAIR-4	38°38′16.9″N 90°09′11.3″W	National stockyards (1st and Last Chance)	Shaded by large trees, several hundred tires, with highly organic contents.	ALB, EPA, TRI, PIP
STCLAIR-5	38°38′47.8″N 90°09′35.3″W	National City (roadside ditch)	Ten tires, discarded containers, weedy area.	ALB
STCLAIR-6	38°37′58.9″N 90°08′27.6″W	9th and Bowman Ave.	Open lot, several tire piles of 10–40; weedy, overgrown with vines.	ALB, EPA, PIP, RES, TER, PUN

* The numbers for the sites in each county match those shown in Fig. 1.

** The 3-letter acronyms correspond to the first 3 letters of the species name: ALB = *Aedes albopictus*; EPA = *Ae. epactius*; PIP = *Culex pipiens*; PUN = *Anopheles punctipennis*; RES = *Cx. restuans*; RUT = *Toxorhynchites rutilus*; SIG = *Orthopodomyia signifera*; TER = *Cx. territans*; TRI = *Ae. triseriatus*.

by Beier and Craig (1985); this was effective for concentrating oocysts but not for quantification of oocysts per infected individual. Mosquito strains were infected by administering doses of approximately 1,000 oocysts per first instar larva in each experimental container. As controls, synchronous cohorts of uninfected larvae of each mosquito strain and species were reared and dissected. The ESL strain of *A. taiwanensis* was introduced to each of the species and strains listed above. The MALAY strain of *A. taiwanensis* was provided to the STCLAIR-2 strain of *Ae. albopictus* as an additional comparison of host-parasite specificity. Finally, infection of *Cx. restuans* was attempted with 2 gregarine species, *A. taiwanensis* ESL and *A. barretti*.

A second set of infections was designed to verify the identification of field-collected *A. taiwanensis* and to estimate oocyst production and viability in both natural and exotic hosts. Oocysts were isolated from 3 field-collected mosquito species and one laboratory-infected species. The infected *Ae. albopictus*, *Ae. epactius* Dyar and Knab and *Ae. triseriatus* were collected from site STCLAIR-4 (Fig. 1, Table 1). The gregarines in *Ae. triseriatus* were identified morphologically as *A. barretti*, while those from the other 2 species corresponded to *A. taiwanensis*. The *Ae. aegypti* WACO strain was infected with oocysts isolated from field samples of adult *Ae. albopictus* from the STCLAIR-4 site. Oocysts from each of the four mosquito species were presented separately to 50 first instar larvae each of *Ae. albopictus* STCLAIR-2 strain and *Ae. triseriatus* WALTON strain. Viability of the oocysts was determined by dissecting 8 fourth instar larvae from each host-parasite combination. Presence of trophozoites in a larva was positive evidence that the source mosquito had passed viable oocysts.

RESULTS

Ascogregarina *identification*: The morphology of the *Ascogregarina* found in East St. Louis *Aedes albopictus* corresponded well to the de-

Table 2. Occurrence of *Ascogregarina* in mosquito species collected from tires in the East St. Louis area.

Mosquito species	No. dissected	Percent positive (*Ascogregarina* species)
Aedes albopictus	366	71 (*A. taiwanensis*)
Ae. epactius	67	42 (*A. taiwanensis*)
Ae. triseriatus	12	58 (*A. barretti*)
Culex restuans	1	{+} (*A. taiwanensis*)
Cx. pipiens	35	0 —
Cx. territans	3	0 —
Orthopodomyia signifera	3	0 —
Anopheles punctipennis	1	0 —

scription of the protozoan by Lien and Levine (1980). Those authors identified the parasite in Taiwan *Ae. albopictus* as different from *A. culicis*, based on morphology and host specificity. Our designation of the gregarine as *A. taiwanensis* was based both on the morphological characterization of Lien and Levine and the cross-infection experiments reported below.

Distribution of gregarines by species and by site: A summary of all gut dissections of field-collected mosquitoes from the East St. Louis sites is shown in Table 2. The mosquito most commonly infected was *Ae. albopictus* with *A. taiwanensis* (Fig. 2 A–C), followed by *Ae. triseriatus* and *A. barretti* (Fig. 2D) and *Ae. epactius* with *A. taiwanensis* (Fig. 3 E–F). A single *Culex restuans* larva was found with a trophozoite with the morphology of *A. taiwanensis*.

In the survey of *Ae. albopictus* in the East St. Louis area, *A. taiwanensis* parasites were found in 5 of 6 sites (Fig. 1, Table 3). In St. Clair Co., 4 sites were positive, with 67–95% of the mosquitoes infected. In larvae, the mean infection intensity among the 4 sites ranged from 22–98 trophozoites per larva, with a maximum of 299 noted in one larva. Of 10 larvae dissected from the MADISON-5 site (in Madison Co.), one larva was found with a single trophozoite. Nonetheless, MADISON-5 was denoted in Fig. 1 as a "negative site" because of this unusually low rate. All other mosquitoes examined from Madison Co. were negative for *A. taiwanensis*. As seen in Fig. 1, the infected and uninfected sites were in close proximity, with the closest pair separated by no more than 2 km.

Pupae and adults of *Ae. epactius* from 2 sites, STCLAIR-4 and MADISON-1, also yielded distinctly different results. While 15 of 16 dissections were positive for *A. taiwanensis* at STCLAIR-4, none of 23 were infected at MADISON-1. Three of those infected at STCLAIR-4 were dead or moribund pupae with very heavy infections (Fig. 3E). The adults had varying manifestations and intensities of infections. Some had very heavy infections, usually with large numbers of gamonts or early gametocysts melanized in the Malpighian tubes (Fig. 3F). Others had light infections with low numbers of stunted trophozoites in the midgut, and still others presented only a few abnormally large trophozoites. Although the larvae of *Ae. epactius* were quite common in tires, the adults were collected more rarely. Compared with *Ae. albopictus*, the *Ae. epactius* adults made up only 4.6% (65/1414) at STCLAIR-4 and 0.3% (3/1,158) at MADISON-1 of the respective samples.

Experimental cross-infections: The reference strains of *Ae. albopictus* showed a 100% infection and very large numbers of trophozoites (up to 1,210), although 2 individuals carried as few as 2 (Table 4). In the 2 strains of *Ae. aegypti*, both the infection rate and number of trophozoites were lower. The pattern of infection was quite aberrant, including oversized trophozoites (Fig. 3C) and, rarely, gametocysts in the midgut. Gamonts (the motile stage in pupae) were frequently melanized in the Malpighian tubes, especially in the dead pupae. In many, a large bolus of both melanized and normal gamonts was present in the posterior midgut near the opening of the Malpighian tubes. Mortality in *A. taiwanensis*-infected *Ae. aegypti* seemed quite high, although unfortunately these trials were not designed for quantitative comparisons.

Variation in infectivity in *Ae. albopictus* was found with respect to both host strain origin and gregarine strain. The ESL strain of *A. taiwanensis* from East St. Louis produced high infections in the 3 USA strains of *Ae. albopictus* (Table 4). The MADISON-1 and NEW-ORLEANS-87 strains showed much higher mean trophozoite load (409 and 499, respectively) than did the STCLAIR-2 strain (86), although the ranges overlapped substantially. The MALAY (from Malaysia) strain of *A. taiwanensis* was also quite infective to the STCLAIR-2 mosquitoes. In 4 larval dissections, the number of trophozoites ranged from 126 to 218. Pupal dissections showed 3 of 3 infected; 2 pupae had all 5 Malpighian tubes infected with 134 and 144 total gametocysts, respectively. These gregarines appeared normal in all developmental stages.

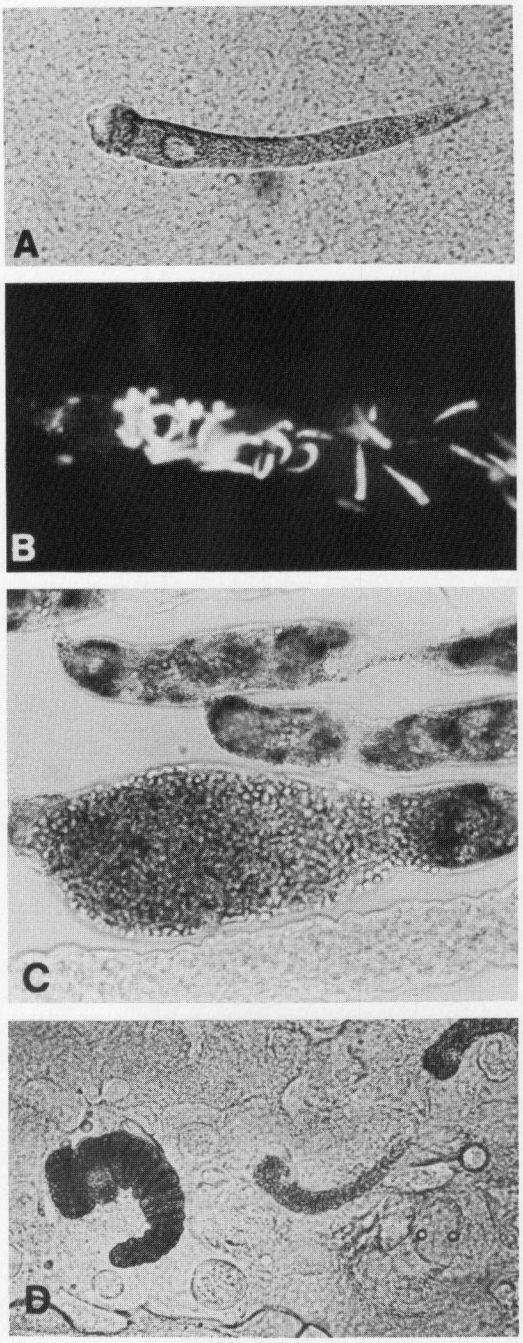

Fig. 2. Natural *Ascogregarina* infections. A. *Ascogregarina taiwanensis* gamont in *Aedes albopictus* larva. B. Darkfield, polarized illumination of heavily infected *Ae. albopictus* larva, showing the birefringent nature of the amylopectin granules in *A. taiwanensis* trophozoites. C. Distal Malpighian tubes of *Ae. albopictus*, one greatly distended by *A. taiwanensis* oocysts. D. *A. barretti* gamonts in *Ae. triseriatus*.

The *Ae. atropalpus* SG strain (from northern Indiana) was also susceptible to infection by *A. taiwanensis* (Table 4). The early infection resembled that of the *Ae. albopictus* STCLAIR-2 strains (Fig 3E). Differences from the normal gregarine development became more pronounced as the larvae matured. In late fourth stage *Ae. atropalpus* larvae, trophozoites exhibited abnormal growth characteristics, often very much larger than normal or very stunted. In pupae, many gamonts were melanized and concentrated in a mass in the midgut at the base of the Malpighian tubes, similar to that noted in *Ae aegypti*. Gametocysts, normally only deep within the Malpighian tubes, were occasionally found in the midgut. In adults, excessively numerous gametocysts (Fig. 3F) and melanized gamonts were often packed in the Malpighian tubes, distorting the normal tubule shape. Most of the *Ae. atropalpus* larvae were moribund when dissected. Although some larval mortality occurred in the *Ae. albopictus* rearing containers, mortality in the *Ae. atropalpus* treatments seemed much higher (again, not quantified).

A third abnormally infected host species, *Ae. triseriatus* WALTON strain, was only slightly susceptible to *A. taiwanensis*, with 1–2 trophozoites per infected larva (Table 4, Fig. 3D). No field infections of *A. taiwanensis* in *Ae. triseriatus* were identified.

In a fourth comparison, field-collected *Cx. restuans* first instar larvae were exposed to *A. taiwanensis* (ESL) and *A. barretti*. None of 43 larvae was infected by *A. barretti*. However, low numbers (1–23) of trophozoites developed in 12 of 22 larvae that were offered *A. taiwanensis* oocysts (Fig. 3, A and B). When pupae and adults of *A. taiwanensis*-exposed *Cx. restuans* were examined, only a single pupa (1/19) contained a gametocyst with normal morphology. None of the adults ($n = 28$) showed signs of a mature *Ascogregarina* infection. In both pupae and adults, trophozoite and gametocyst melanization was in evidence.

Oocyst numbers and viability of cross-infections: Field collections of *Ae. albopictus*, *Ae. epactius* and *Ae. triseriatus* from East St. Louis all produced oocysts in sufficient numbers to be concentrated by the isolation procedures of Beier and Craig (1985). The more heavily infected *Ae. albopictus* produced a concentrate of 5,000 to 30,000 oocysts per ml, while the concentrate from the more lightly infected *Ae. epactius* and *Ae. triseriatus* contained no more than 1,000 per ml. (Note that the infections in *Ae. triseriatus* were identifiable as *Ascogregarina barretti*.) We were able to discern oocysts in the concentrate from the experimentally infected *Ae. aegypti* WACO strain; nonetheless, the con-

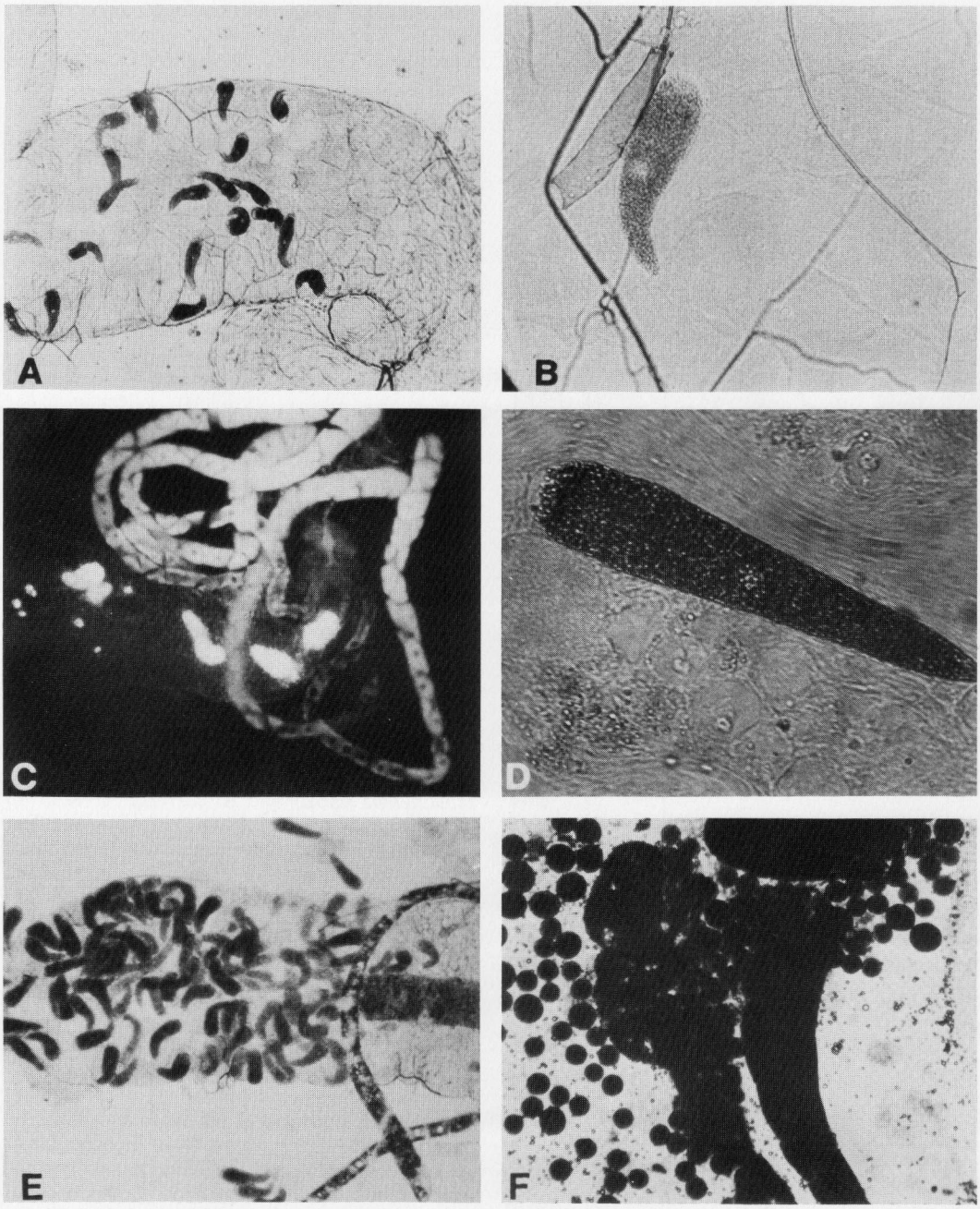

Fig. 3. Experimental *Ascogregarina* infections. A–B. *Ascogregarina taiwanensis* in *Culex restuans* larva: A. Posterior midgut with trophozoites. B. Single trophozoite with fourth stage larval antenna for size comparison. C. enlarged trophozoite in larval midgut of *Aedes aegypti* (darkfield illumination). D. *A. taiwanensis* trophozoite in larval *Ae. triseriatus*. E–F. *A. taiwanensis* in *Ae. atropalpus*. E. Heavily infected larval midgut. F. Numerous gametocysts freed from broken Malpighian tubes.

densed slurry was fed to the *Ae. albopictus* and *Ae. triseriatus* trial organisms.

The infectivities of the extracted oocysts are summarized in Table 5. The *A. taiwanensis* oocysts from field *Ae. albopictus* and *Ae. epactius* were very infective to *Ae. albopictus*. *Ascogregarina barretti* showed a normal level of infection in *Ae. triseriatus*, but was not infective

Table 3. *Ascogregarina* infection intensities in *Aedes albopictus* as distributed among collecting sites in the East St. Louis area.

County -site	No. dissected*	Infected %	Trophozoites in larvae		
			No. larvae	Mean	Range
STCLAIR-2	70	89	26	52	4–299
STCLAIR-4	135	95	29	54	5–230
STCLAIR-5	9	67	4	98	4–227
STCLAIR-6	19	95	7	22	1–48
MADISON-1	76	0	0	—	—
MADISON-2	10	{+}	1	1	—

* Includes larvae, pupae and adults.

Table 4. Experimental infections by *Ascogregarina taiwanensis* from East St. Louis in strains of *Aedes albopictus*, *Ae. aegypti* and *Ae. atropalpus*. The *Ae. triseriatus* bioassay data (Table 5) are included for comparison.

Strain	Larvae dissected		No. of trophozoites	
	No.	% positive	Mean*	Range
Aedes aegypti				
ROCK	16	56.3	40	5–110
WACO	25	12.0	17	5–24
Aedes albopictus				
STCLAIR-2	8	100.0	86	2–271
MADISON-1	5	100.0	409	72–1,210
NEW-ORLEANS-87	5	100.0	449	2–722
Aedes atropalpus				
SG	11**	90.1	85	14–225
Aedes triseriatus				
WALTON	16	25.0	1.5	1–2

* Calculations include only infected larvae.
** Eight of the 10 infected larvae were moribund.

Table 5. Bioassay for viability of oocysts using *Aedes albopictus* STCLAIR-2 strain and *Ae. triseriatus* WALTON strain. A. *Ascogregarina* oocysts isolated from East St. Louis field samples of *Aedes albopictus* (ALB), *Ae. epactius* (EPA) and *Ae. triseriatus* (TRI). B. *Ascogregarina taiwanensis* oocysts from East St. Louis passaged through *Ae. aegypti* WACO (AEG).

Oocyst origin	Bioassay host	No. dissected	Percent infected	Range (trophs/larva)
A. East St. Louis field oocysts				
ALB*	*Ae. albopictus*	8	100	35–311
ALB*	*Ae. triseriatus*	16	25	1–2
EPA*	*Ae. albopictus*	8	100	10–121
EPA*	*Ae. triseriatus*	8	0	0
TRI**	*Ae. albopictus*	8	0	0
TRI**	*Ae. triseriatus*	8	88	8–175
B. Laboratory passaged oocysts				
AEG*	*Ae. albopictus*	8	25	2–6
AEG*	*Ae. triseriatus*	8	0	0

* Infections were identified as *Ascogregarina taiwanensis* from morphology of trophozoites in larval dissections.
** Infections identified as *A. barretti*.

to *Ae. albopictus*. *Aedes aegypti* also produced a low level of viable *A. taiwanensis* oocysts capable of infecting *Ae. albopictus*. Although *Ae. triseriatus* was slightly susceptible to *A. taiwanensis* from *Ae. albopictus*, oocysts from neither *Ae. epactius* nor *Ae. aegypti* resulted in discernible infection in *Ae. triseriatus* larvae.

DISCUSSION

Ascogregarina taiwanensis is probably present in many North American populations of *Ae. albopictus*. Subsequent to its discovery in East St. Louis, one of us (D.M.W.) identified this parasite/mosquito combination at 3 additional sites—Chicago, Illinois, Polk County, Florida,

and Potosi, Missouri. Nonetheless, the gregarine in East St. Louis is not uniformly distributed in spite of the close proximity of the sites (Fig. 1, Table 3). This is probably due to "founder effect," where the populations at each site were founded by mosquitoes of a different origin and with very different levels of gregarine infection. Subsequently, the infected mosquitoes did not disperse into the Madison Co. sites from the sites in St. Clair Co., only 2 to 3 km distant.

Low dispersal capability of *Ae. albopictus* has been measured in several field release studies (Hawley 1988). Electrophoretic data from samples within and between cities in the United States have indicated both founder effects among cities and lack of genetic similarity between adjacent tire sites (Black et al. 1988). Origin of tires (local or purposely transported) and reasons for tire placement (discards on rubbish heap, tires for resale, tires for processing) seem to be more important for dispersal than movement of the mosquito through the environment. If this is the case, then finding of disjunct distributions of the *Ascogregarina* is not surprising.

Although the gregarine-positive and negative populations of *Aedes albopictus* are probably of different geographic origins, how can the gregarine be absent from any site, given its high rate of infection in the St. Clair Co. sites and the intense level of induced infection in mosquitoes from the MADISON-1 site? Two scenarios can be constructed. The first is as follows: If uninfected individuals are more reproductively fit than infected, uninfected individuals can expand throughout a site at a greater rate than the infected individuals. In new colonizations the gregarine may not be capable of spreading quickly through a rapidly expanding host population. If sampling of the population occurs during the expansion phase, the gregarine may escape detection. Data from other mosquito-gregarine systems do not support this interpretation—generally, the gregarine has little effect on its natural host (Beier and Craig 1985). For the *A. taiwanensis-Ae. albopictus* association, however, some larval and pupal mortality seems to occur in laboratory infections (D. M. Wesson, unpublished observations). The relevance of this laboratory mortality to effects on reproductive fitness in the field remains to be investigated.

Alternatively, the uninfected population may consist of individuals genetically resistant to parasitization. As the gregarine oocysts are introduced to resistant mosquitoes, they are neutralized in some manner. However, for the Madison Co. populations, this explanation is unlikely. The MADISON-1 strain, derived from the uninfected site, proved very receptive to laboratory infections.

In the field populations where it was found, *A. taiwanensis* was highly infectious. Infection rates ranged from 67 to 95%, compared to natural infection levels of 60% for *A. barretti* (Beier and Harris, 1983), 70% for *A. culicis* (Barrett et al. 1971) and 28% for *A. clarki* (Sanders and Poinar 1973). In addition, *A. taiwanensis* has a demonstrated capacity to pass through at least one generation in non-*Ae. albopictus* mosquito hosts. This has not been demonstrated in other mosquito gregarines and lends a new dimension to its survival potential. The *A. taiwanensis* described from Taiwan apparently did not show this capability. Even though 48% of *Ae. aegypti* larvae carried trophozoite stages in laboratory infections, no infectious oocysts were produced (Lien and Levine 1980). Since the U.S. *Ae. albopictus* are thought to have been introduced from mainland Japan (Hawley et al. 1987), the associated gregarine may be quite different from the Taiwan gregarine with respect to its developmental capabilities in exotic hosts.

The extent to which *A. taiwanensis* has deleterious effects on *Ae. albopictus* and sympatric container-breeding mosquitoes is still unknown. Our initial observations indicate that (at least in the exotic mosquito hosts *Ae. aegypti* and *Ae. epactius*) *A. taiwanensis* may have a significant effect on mosquito survival.

ACKNOWLEDGMENTS

We thank J. F. Cully, Jr., and G. B. Craig, Jr., for reading the manuscript and offering suggestions for improvement. We also thank other members of the Vector Biology Laboratory—W. Hawley, C. Pumpuni, S. Hanson, T. Streit and M. Niebylski—for assisting in confirmatory field collections. This work was supported by NIH grant AI-02753 and NIH Training Program 2 T32 AI-07030.

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